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Sex Ratio, Size at Reproductive Maturity, and Reproduction of the Hawaiian Kona Crab, *Ranina ranina* (Linnaeus) (Brachyura, Gymnopleura, Raninidae)[1]

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ABSTRACT: Sex ratio and size at reproduction of *Ranina ranina* (Linnaeus) in Hawaii were investigated. A sample of 1596 Kona crabs collected over 1 year in Hawaiian waters was examined to determine sex ratio and size at reproduction.

Males constituted 55 percent of the overall samples and a similar proportion in all size classes. Males attain a larger maximum size than do females and have mature spermatozoa when their carapace length exceeds 60 mm. Secondary sexual characteristics in the male develop at a carapace length of about 75 mm.

Females are ovigerous from May to September. Most ovarian growth occurs between February and May. In May, at the beginning of the spawning season, the number of eggs ovulated is a function of maternal body size: a 25-percent increase in carapace length is associated with a 200-percent increase in number of eggs ovulated. This is not so later in the spawning season (August–September). Larger females appear to ovulate at least twice each season, with the primary effort going into the first ovulation. The smallest 5-mm size class in which at least 50 percent of the females are ovigerous during the spawning season is 70.0–74.9 mm in carapace length. The mean minimum size of ovigerous females is 86 ± 8 mm in this dimension. The spermatheca in females is open to the outside at carapace lengths exceeding 60 mm.

Eighteen crabs with carapace lengths less than 65 mm were captured. Half (31.9 mm–42.6 mm) were white in color and were all immature; the remaining half (43.6 mm–61.1 mm) were the usual orange color and all of these exhibited active gametogenesis. This correlation of color with size may be of significance for reproductive behavior.

Ranina ranina (Linnaeus), commonly referred to in Hawaii as the Kona crab, is found throughout the Indo-Pacific. In Hawaiian waters, it is found at depths between 6 m and 200 m, where it burrows in sandy ocean bottoms. The systematic position of the family Raninidae, of which *R. ranina* is the type genus, was recently reviewed by Števčić (1973).

Because *R. ranina* is fished commercially in Hawaii, Onizuka (1972) investigated the reproduction, growth, migrations, sex ratio, and size frequency of Kona crabs in Waimea and Waialua bays on Oahu, Hawaii. For that report, observations were made over a 3-year period (1966–1969) and were tabulated by month but not by year. No indication was given that samples were taken every month over the 3 years. It would have been useful if the data had been tabulated on a yearly basis, because then any yearly fluctuations in sex ratio or size frequency might have been determined. Also, information was not included on the frequency of ovigerous females in various size classes, which would have provided a measure of the size at reproduction. Onizuka (1972) stated that rearing studies indicated that female Kona crabs ovulate twice in summer, but the sizes of females that ovulated twice were not reported.

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Our inquiry was directed toward the sex ratio, size distribution, annual reproductive cycle, general development, size at reproduction, and sexual dimorphism of *R. ranina* in Hawaii. We were limited in the sampling program to collections made aboard a commercial crab-fishing boat; site, time, and technique were determined by that operation.

METHODS

Animals used in this study were collected from Penguin Banks, west of the island of Molokai, Hawaiian Islands, an area of approximately 350 square miles, which is shallow (average depth 60 m) relative to surrounding water (average depth 600 m). Large numbers of Kona crabs were trapped along the outside edge of the banks at depths of 100–200 m.

Crabs were caught by entanglement in traps laid along the bottom on a line. Traps were made by stretching two layers of 5-cm nylon mesh over 1-meter-diameter metal hoops, and were baited with tuna scraps. Usually, 80 traps were attached to a longline at intervals of about 12 m, and were set for 45 minutes. The animals were held in running seawater in a large deck box until they were transferred to the running seawater system at Kewalo Marine Laboratory in Honolulu. Ordinarily, on a commercial crab-fishing boat many undersized crabs and all ovigerous females are released upon capture. However, because population data were being gathered, all crabs caught were measured and sexed.

Measurements were made with direct-reading metric calipers to the nearest 0.1 mm. Carapace length was chosen as the reference measurement, and was defined as the distance in millimeters from the posterior margin of the right orbit to the central posterior margin of the carapace (Figure 1*A*). Onizuka (personal communication) used the same measurement. Chelar length was measured along the outer surface of the propodus of the right chela, as illustrated in Figure 1*B*.

The data were arranged into 5.0-mm size classes based upon carapace length. When available, at least five members of each sex in each size class were dissected within 3 days of capture. Histologically, males were considered to be mature when the sperm ducts contained mature spermatozoa; females were judged to be mature when vitellogenesis was apparent in the ovaries. Fresh ovaries were wet-weighed to the nearest 0.1 g.

Embryo masses (sponges) were removed from the abdomens of ovigerous females, blotted, and weighed. Samples of approximately 150 embryos were taken from each of them, weighed to the nearest 0.001 g, and the exact numbers of embryos counted. In this fashion, an average weight per embryo was obtained and used to calculate the number of embryos in each sponge.

RESULTS

Sex Ratio and Size Distribution

Information on population structure was derived from analysis of 1596 crabs, 55 percent of which were males (chi-square test at the 0.01 level indicates a significant deviation from a 1:1 sex ratio). Similar sex ratios were reported by Onizuka (1972) and were also significant at the 0.01 level. The size frequency of male and female crabs in this study is compared to those reported by Onizuka (1972) in Figure 2. Males attain a greater maximum size than do females and predominate in the larger size classes; whereas females are predominant in the smaller size classes. The Kolmogorov-Smirnov two-sample test (Siegel 1956: 127–136) indicates that the Penguin Banks, Waimea Bay, and Waialua Bay populations have different size distributions. Waimea Bay has the greatest proportion of small crabs; Penguin Banks, the greatest proportion of large crabs; and the Waialua Bay population lies between these two, with the largest proportion of crabs in the middle size classes.

Sexual Dimorphism

The male abdomen is narrower than that of the female of a similar carapace size, even in the smallest crabs caught in this study. All males, including immature ones, have the first two pairs of pleopods modified into a pair of copulatory organs. A gonopore is found on each

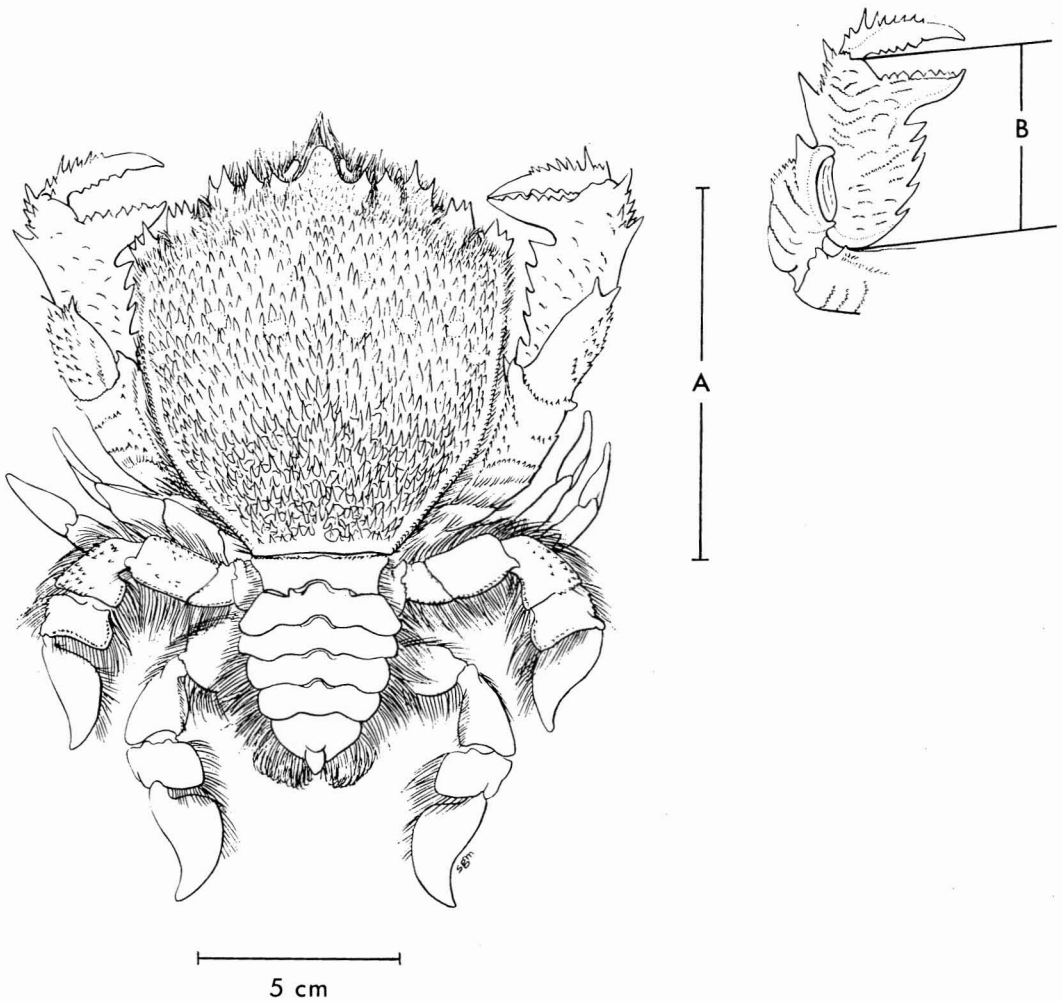

FIGURE 1. *Ranina ranina* (L.). Dorsal view of a mature male, illustrating the measurements used in this study. *A*, carapace length; *B*, right chelar propodus length.

of the coxae of the fifth pair of legs in males, and each gonopore is associated with an external papilla. All females have visible gonopores on the coxae of the third pair of legs, and mature females have an external spermatheca located medially on the (seventh) sternites between the third and fourth pairs of legs (Gordon 1963). How fertilization is accomplished was not determined.

Males attain a larger maximal size than do females (Figures 2, 3). Males of at least 75-mm carapace length have larger anterolateral carapace spines, larger chelae, and setae on the palmar surface of the dactyli and propoda of the chelae. All of these characteristics become more prominent with increasing size. This is illustrated for chela length in Figure 4. The chelar propodus in both sexes exhibits positive allometric growth (allometric coefficient, $a = 1.14$) up to a carapace length of about 70 mm, at which size the growth of the chelar propodus in females adjusts to a new allometric rate ($a = 1.20$). For males larger than 70 mm, this structure continues to increase geometrically.

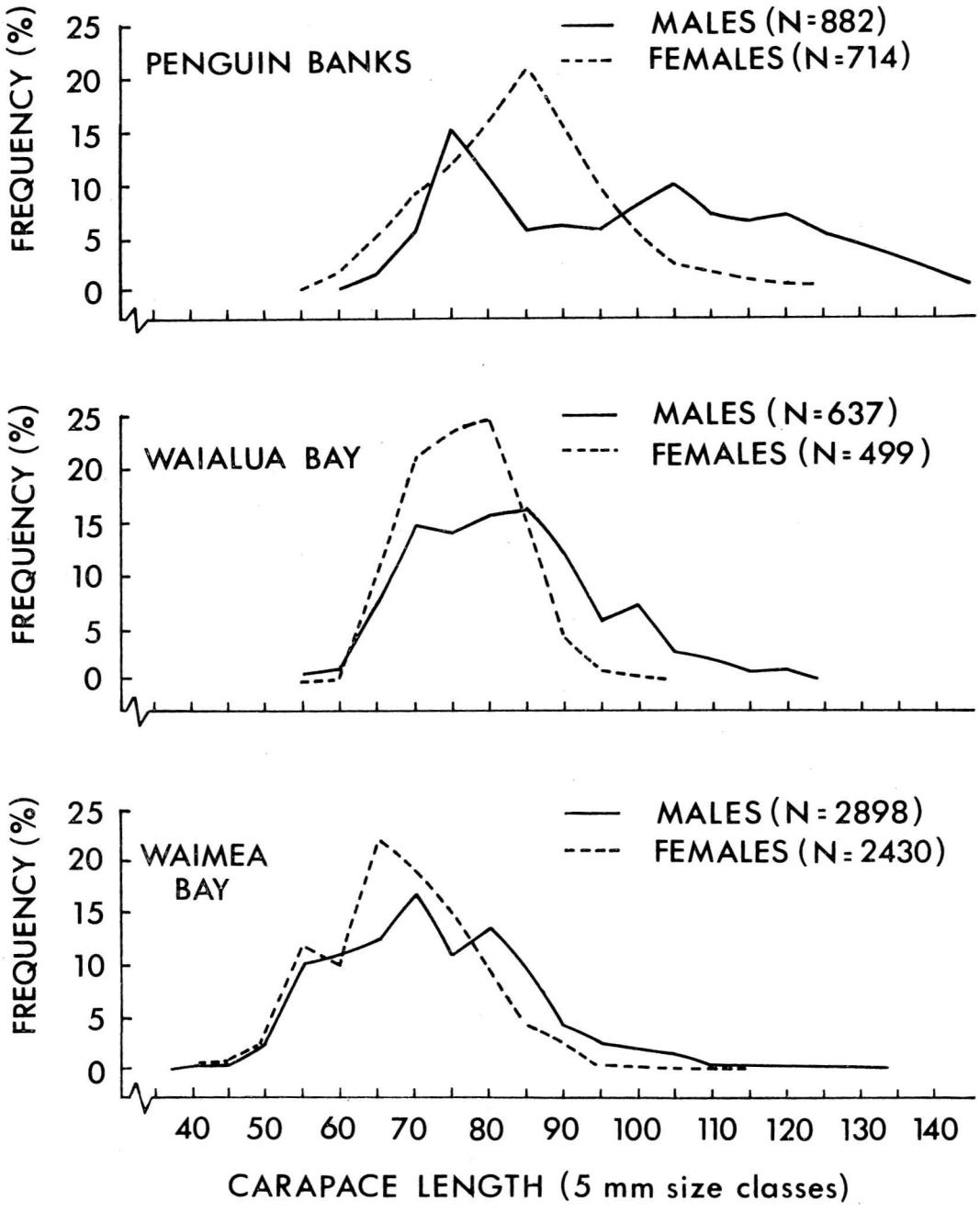

FIGURE 2. *Ranina ranina* (L.). Size frequency distributions. Comparison of Penguin Banks population (this study) with those of Waimea and Waialua bays (Onizuka 1972). Because of ambiguity in one collection, only 714 females were included in this graph rather than the 791 collected, as indicated by the total in Figure 5.

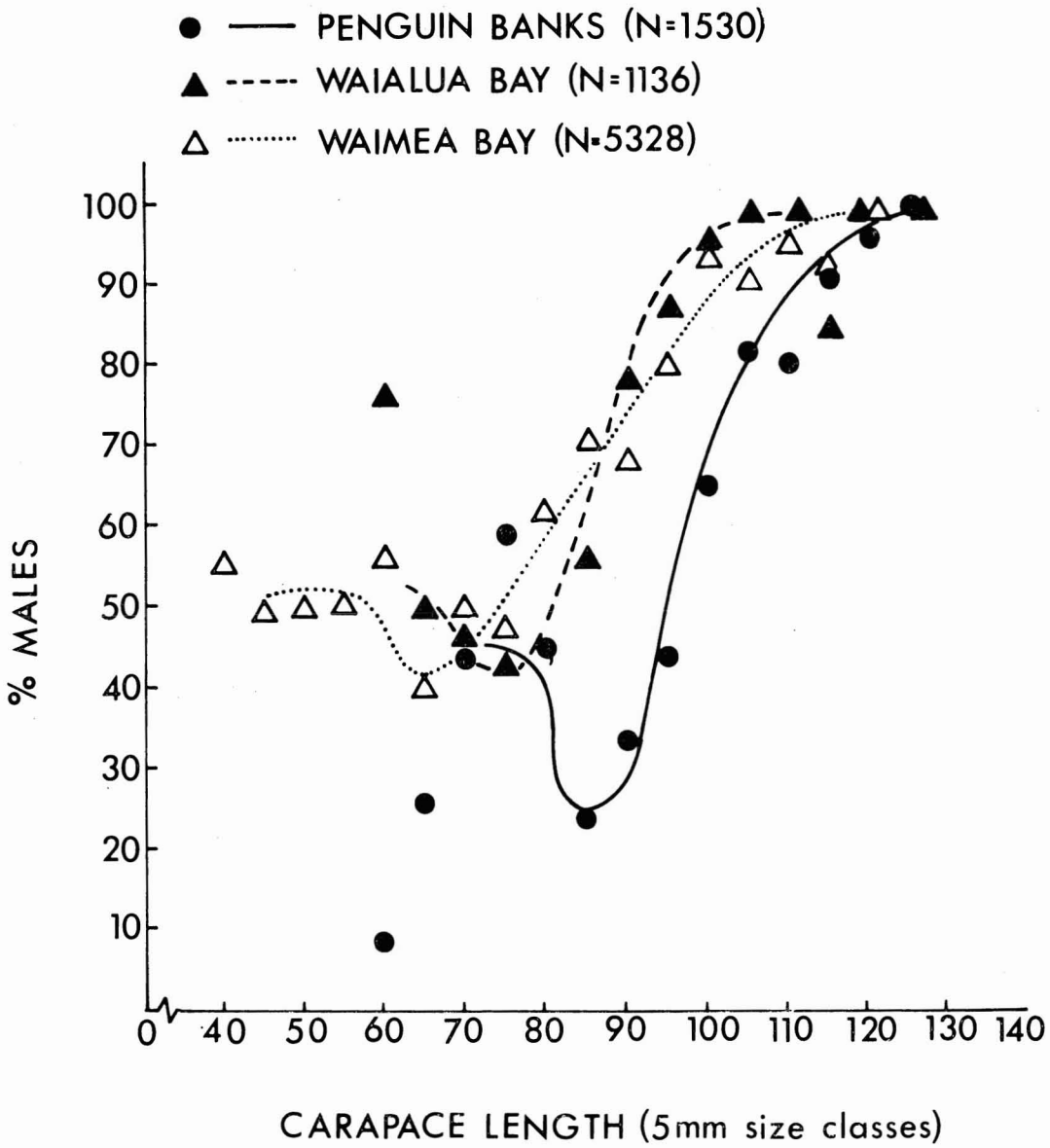

Figure 3. *Ranina ranina* (L.). Sex ratio as a function of size. Comparison of Penguin Banks population (this study) with those of Waimea and Waialua bays (Onizuka 1972). The 60-mm size class values for Penguin Banks and Waialua Bay are based on only 12 and 9 animals, respectively. The curves were fitted by inspection.

Reproduction

Female R. *ranina* are ovigerous during the summer months in Hawaii (Figure 5). In 1973, ovigerous females were caught initially on 25 May. Ninety-six percent of all females captured at that time were ovigerous, and all embryos were in an early stage of development. This suggests that ovulation was approximately simultaneous for the entire population. In Figure 6, the regression line for May values indicates that at the beginning of the spawning season in May, the number of embryos per sponge is a function of maternal size, i.e., larger

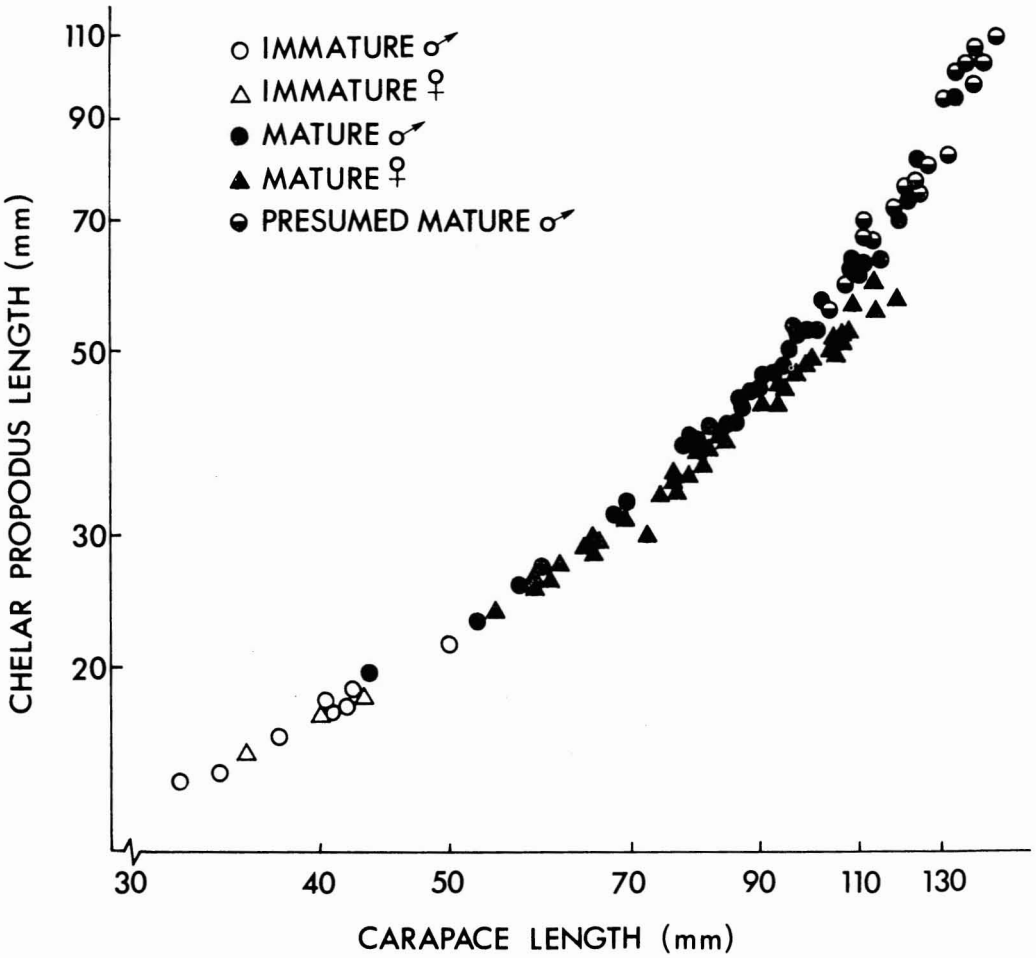

FIGURE 4. *Ranina ranina* (L.). Relative growth in length of the right chelar propodus. The symbols reflect maturity based upon histological examination of the gonads. The males presumed mature were not dissected.

females ovulate a greater number of eggs. However, at the end of the spawning season in August and September the number of embryos per sponge appears to be unrelated to body size. Of nine August–September estimates of embryo number, only two are similar to May values, the remaining seven being lower. The numbers of embryos per sponge estimated by Onizuka (1972) for the Kona crab populations of Waialua and Waimea bays are considerably lower than the estimates of this study. Perhaps this may be accounted for by the difference in estimating techniques, an inconsistency we could not resolve as Onizuka did not report sponge weights.

Ovarian growth was monitored from February to September 1973. Ovigerous females examined in May had heavier ovaries than did those of similar size captured in August and September. This is especially marked in the larger size classes (Figure 7). Ovigerous females caught in August had ovarian weights similar to those of females captured in September, and ovarian weights for any size class were similar in February and August–September. This suggests that between the end of the spawning season in September and the following February, little ovarian growth occurs. Ovarian weights in March for any size class were greater than those in February, indicating that most

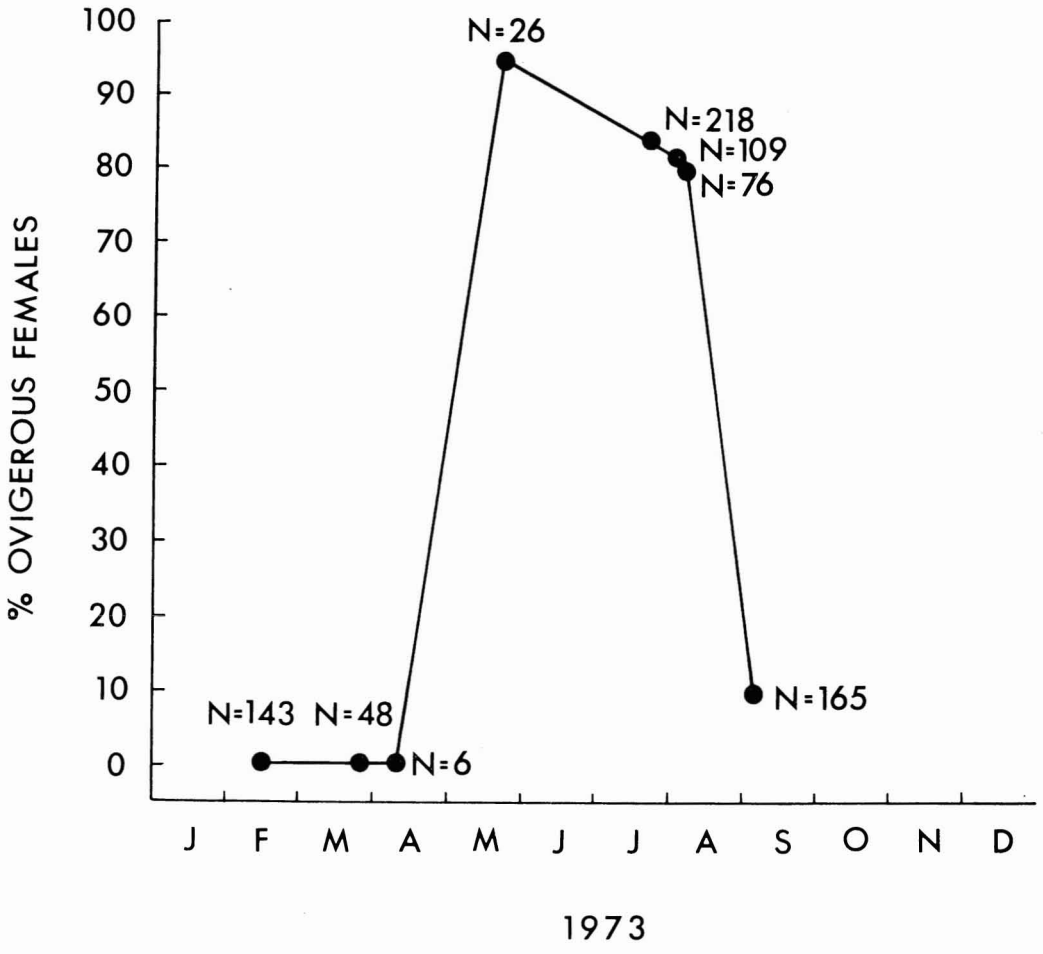

Figure 5. *Ranina ranina* (L.). Frequency of ovigerous females (regardless of size) during the period February to September 1973. (N = 791 females.)

ovarian growth for the summer spawning season occurs after February.

By determining the frequency of ovigerous females in several size classes, one should be able to ascertain the size at which reproductive maturity occurs. In addition to our histological estimate of size at reproductive maturity, we compared two such size estimates of initial reproductive activity. (1) Minimum size class at reproduction was defined as the smallest 5-mm size class in which at least 50 percent of the females were ovigerous. For the Penguin Banks population (Figure 8), this criterion was met only by females with carapace lengths in the size class 70.0–74.9 mm or larger. (No females smaller than 60-mm carapace length were caught during the spawning season.) (2) Mean minimum size of sexual maturity was determined by the method of Wenner, Fusaro, and Oaten (1974), in which a cumulative normal distribution of ovigerous females is plotted on probability paper; a line was fitted to these points by inspection, and the 50-percent value and standard deviation then were read directly from the abscissa (Figure 9). By this method, a value of 86 ± 8 mm was obtained for mean minimum size of sexual maturity in females.

The spermatheca of the female, which presumably is the site of sperm reception, does not become apparent externally until about 60-mm

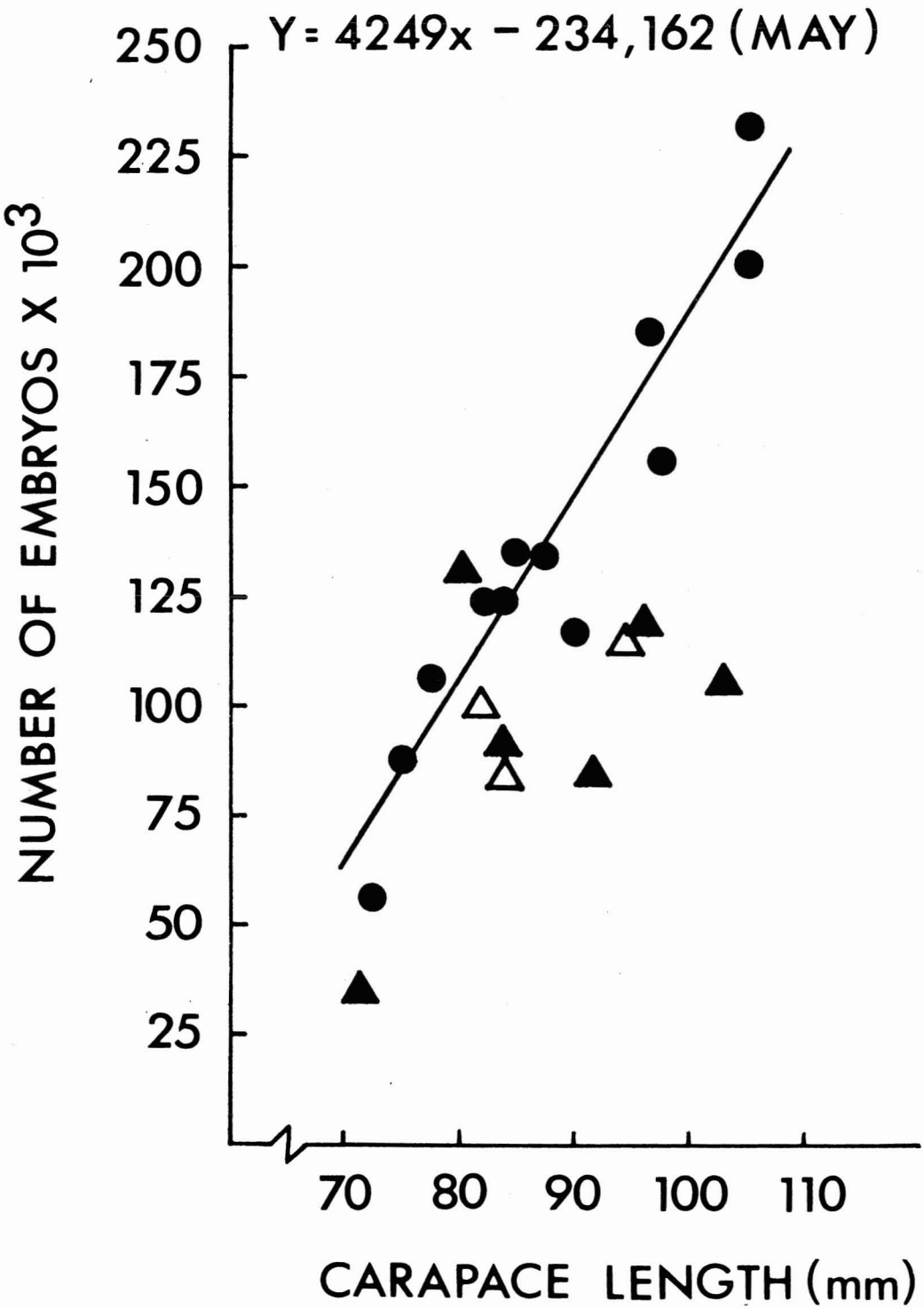

FIGURE 6. *Ranina ranina* (L.). Number of embryos per sponge as a function of maternal carapace length. Specimens were collected during May (solid circles), August (open triangles), and September (solid triangles), 1973. The regression line is for May values.

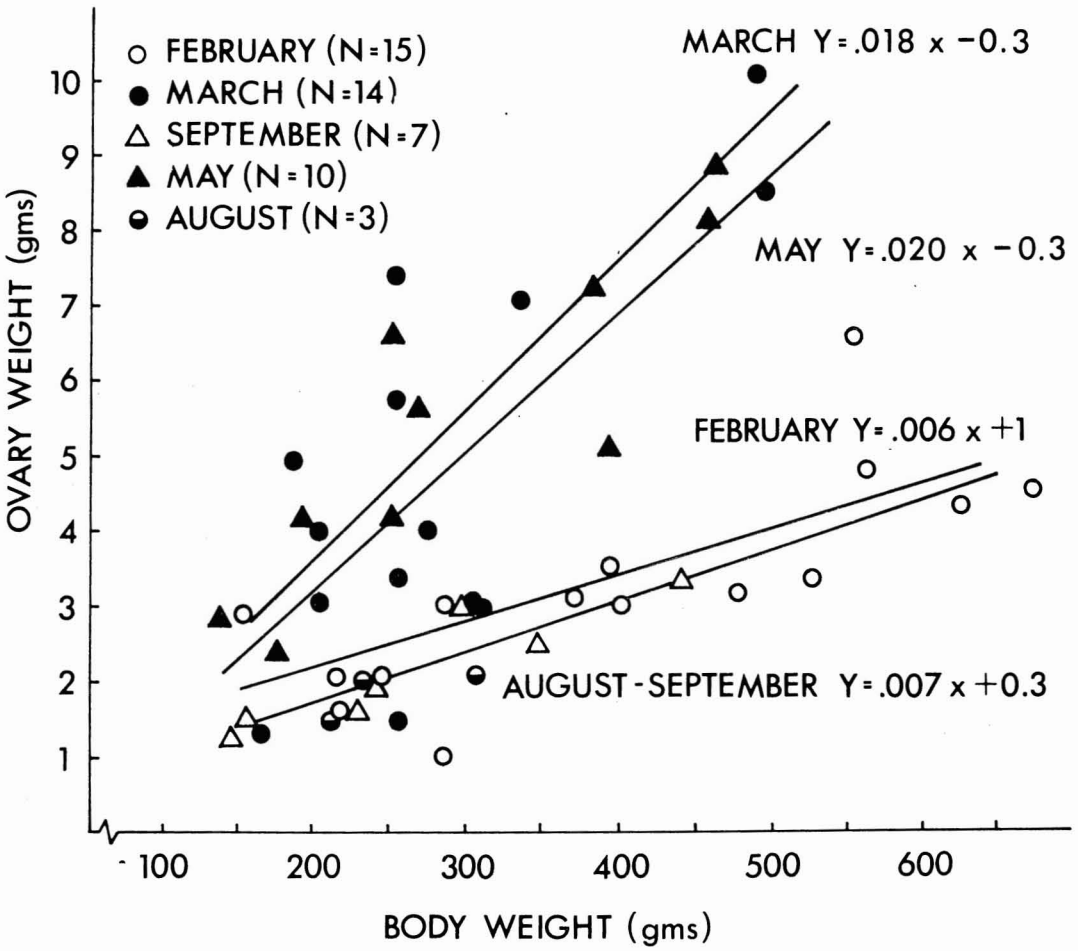

Figure 7. *Ranina ranina* (L.). Ovary weight as a function of body weight and time of year. Only females from Penguin Banks with carapace lengths > 60 mm are included. Females recorded for May and September were ovigerous. Sponge weight is excluded.

carapace length. The smallest ovigerous female captured in this study was 65 mm in the reference dimension. Onizuka (1972) reported a carapace length of 63 mm for the smallest ovigerous female. Gordon (1963) referred to a female of 63-mm carapace length as "very immature," but she did not report the condition of the gonad. The spermathecal opening of that specimen (p. 54, fig. 12*A*) was evident externally.

Although we were not able to determine the size at which males copulate, we were able to determine the size at which they have mature spermatozoa. Immature males have small transparent sperm ducts; mature males have large ones, packed with mature spermatozoa, which give the ducts an opaque white appearance. Viewed microscopically, mature spermatozoa are highly refractile, whereas the immature germinal cells are not. Mature spermatozoa are aflagellate, round, with four cytoplasmic rays, and, in gross morphology, resemble those described for other Brachyura (Binford 1913; Fasten 1926). Ryan (1969), however, has reported that they are unlike other brachyuran spermatozoa in ultrastructure. All males with carapace lengths >60 mm in this study had mature spermatozoa.

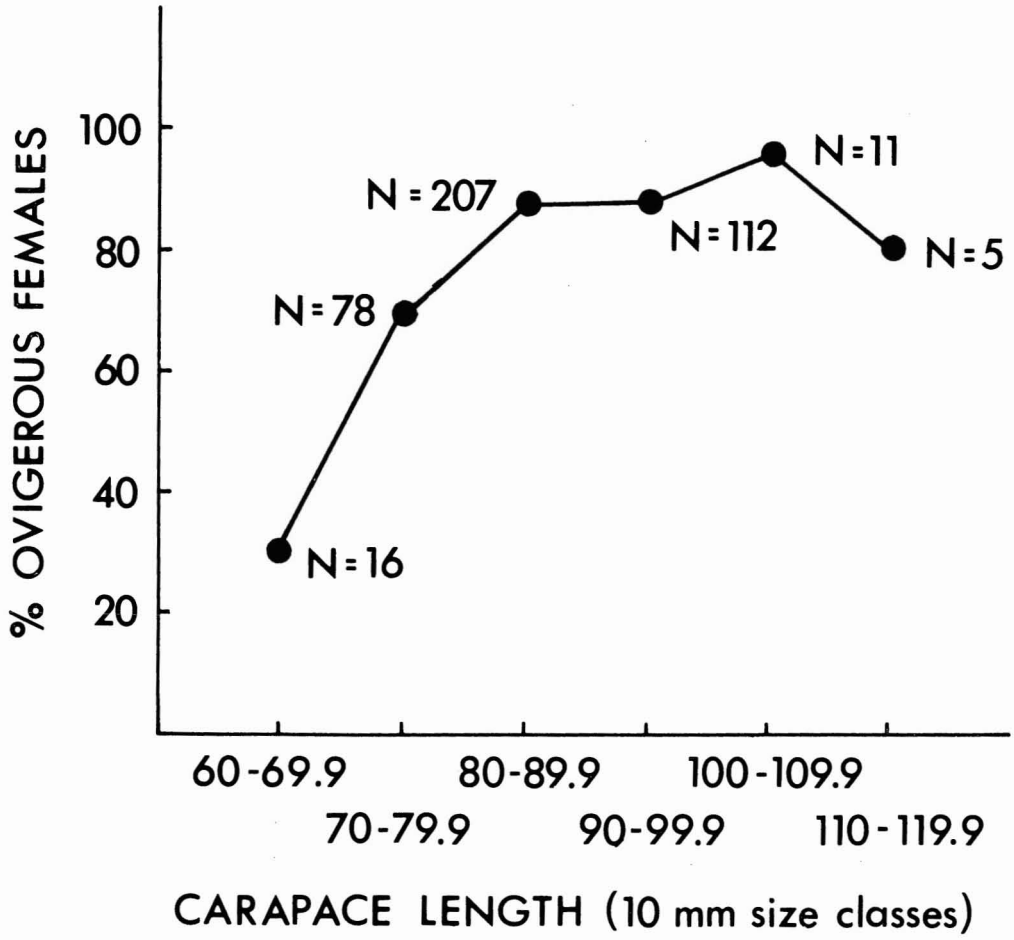

FIGURE 8. *Ranina ranina* (L.). Frequency of ovigerous females as a function of size for the Penguin Banks population, from 25 May to 5 August 1973.

Development

Gross observations were made on developing embryos and compared with those described by Boolootian et al. (1959) for five species of west coast (United States) crabs. Development of Kona crabs does not differ markedly, except that Kona crab embryos lack extensive pigment bands. Also, the yolk mass does not separate into two portions; when the larvae hatch, they still have yolk; whereas none was reported for the crabs described by Boolootian et al. (1959). An examination of embryos from two females indicated that embryonic development occurs in 27 days at 24° C. Onizuka (1972) reported an average of 29 days with a range of 24–35 days.

In our study, some larvae survived two molts. The first molt occurred 7–8 days after hatching and the second about 14 days after hatching. Sakai (1971) reported the first molt at 4–5 days and the second one 5–6 days later. We compared larvae from the hatch and first molt to larvae described by Sakai (1971) and found that gross structures were identical to his zoeal stages I and II, respectively.

DISCUSSION

Sex Ratio and Size Distribution

Our observation that there are more males than females (55 and 45 percent, respectively)

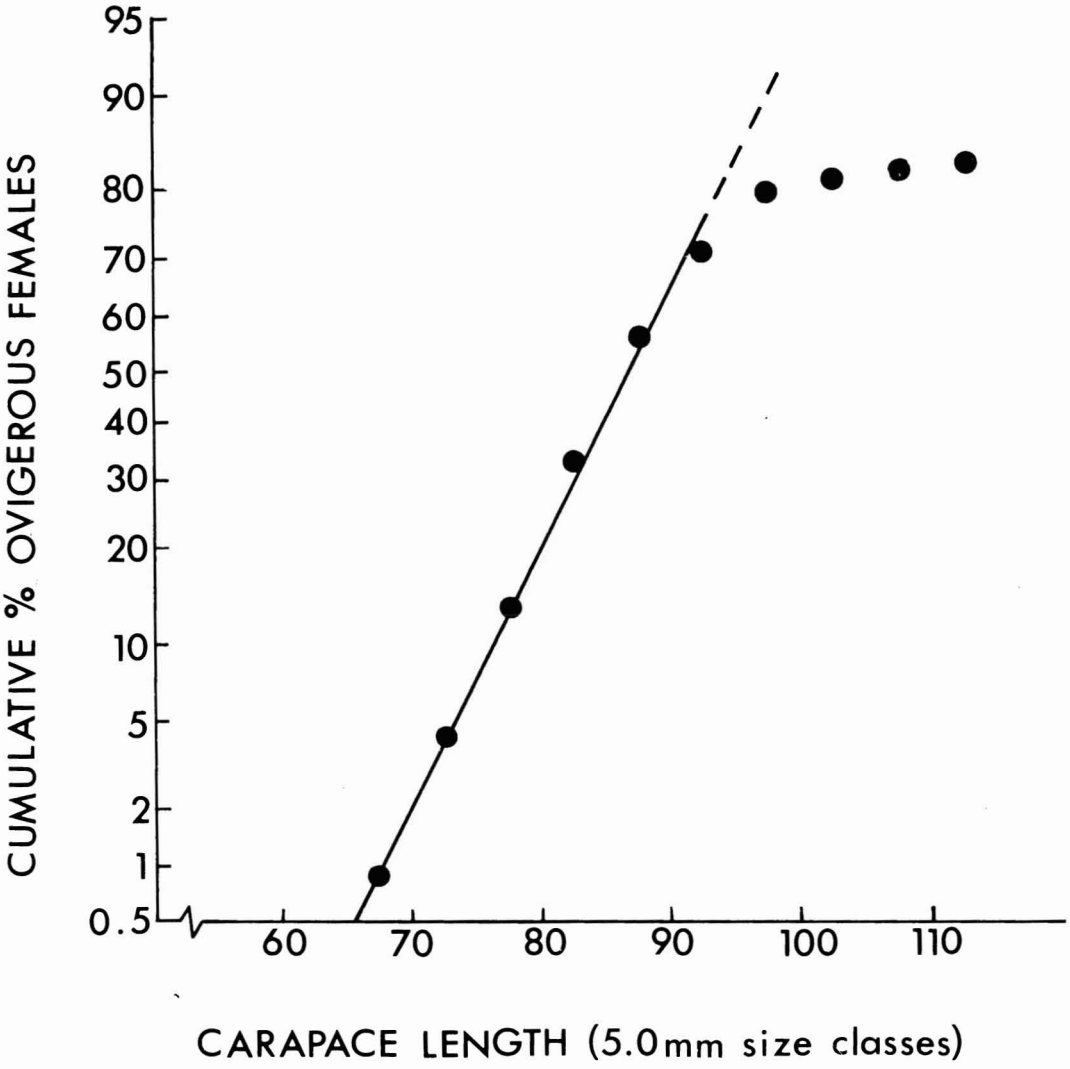

Figure 9. *Ranina ranina* (L.). Mean minimum size of ovigerous females, given by comparing carapace length size classes with cumulative percentage of ovigerous females.

is consistent with data from the two bays studied by Onizuka (1972). He reported sex ratios of 56-percent males in Waialua Bay (N = 1136), and 54-percent males in Waimea Bay (N = 5328). Wenner (1972) reviewed this topic and reported that a deviation from a 1:1 sex ratio is not unusual among marine Crustacea. This study probably contains a sampling error, if animals of less than 70-mm carapace length are considered. We caught very few small animals at Penguin Banks, whereas Onizuka (1972) caught a large number of small animals in Waimea Bay but not as many in Waialua Bay. Several factors could account for this. Obviously, small crabs are more likely to escape entanglement in the 5-cm mesh of the traps. Also, extensive fishing pressure probably preferentially removes members of the large size classes, as fishermen fish for large crabs. Crabs caught at Waialua and Waimea bays, which generally have quiet water and are close to shore, are smaller than those caught at Penguin Banks

where the water is less protected and farther from shore and populated areas. The bays studied by Onizuka (1972) are very accessible to sport fishing, but a true measure of the fishing pressure in those areas was not available.

When sex ratio is plotted as a function of size for the populations of Penguin Banks, and Waimea and Waialua bays, a pattern emerges (Figure 3), which Wenner (1973) called "anomalous." A possible explanation for the decrease in percentage of males is that the male and female growth rates differ. If this reasoning is correct, males of 80–90-mm carapace length may grow more rapidly than would females of similar size. The probability of obtaining males of that size would be reduced accordingly. This explanation may be correct, because Onizuka (1972) reported that mature males grow an average of 9.9 mm per molt, whereas mature females show an average increment of 7.5 mm. If intermolt periods are of equal duration in each sex, this variation in growth rate could explain both the decrease in the percentage of males in the lower size classes and the preponderance of males in the larger size classes. The observation that male and female growth rates diverge between 80 and 90 mm carapace length (Figure 3) is consistent with the 86 ± 8 mm value for mean minimum size of reproductive maturity for females (Figure 9). Presumably, mature females put more energy into reproductive growth than into somatic growth.

Sexual Dimorphism

Secondary sexual characteristics that the male Kona crab develops at about 75-mm carapace length (large anterolateral spines and chelae) become so prominent as to give the anterior portion of the body a square and formidable appearance. These characteristics may be involved in mate selection and/or aggressive interactions involving competition for food and/or space. Hartnoll (1974) has discussed the relative growth patterns for several such features in a variety of crabs. Chelar growth in immature and mature Kona crabs follows a similar pattern, except that for males with carapace lengths $\geqslant 70$ mm, growth of the chelar propodus is not by simple allometry (Figure 4). This is similar to chelar growth described for the Hawaiian ghost crab, *Ocypode ceratophthalmus* (Pallas) (Haley 1973).

Reproduction

During the summer (25 May–5 August) of 1973, an average of 86 percent of the females with carapace lengths $\geqslant 60$ mm were ovigerous. During the remainder of the year no females were ovigerous. Onizuka (1972) reported essentially the same pattern, except that the ovigerous crabs averaged 67 percent in June and July, a lower percentage than that found at Penguin Banks. Furthermore, Onizuka (1972) found a few females with carapace lengths greater than 65 mm during the summer that did not have developing ovaries or were not ovigerous. Every female dissected in this study, with carapace length > 54 mm, from May to August had developing ovaries and/or was ovigerous. The females Onizuka (1972) referred to as immature (i.e., had no developing ovaries and were not ovigerous) may simply have finished spawning. Onizuka did not report the months during which these females were caught.

Body size and time of year determine the number of embryos per sponge (Figure 6), and body size has a marked effect on the number of embryos early in the breeding season. In this study, a 25-percent increase in carapace length was associated with a 200-percent increase in number of embryos per sponge. In the study by Onizuka (1972), a 25-percent increase in carapace length was associated with a 100-percent increase in number of embryos. That the crabs in Waialua and Waimea bays had fewer embryos per sponge may be due to a difference in estimating technique, or it could be a real difference and may have reflected insufficient food for comparable reproductive growth in those populations.

Females sampled late in the breeding season tended to have fewer embryos per sponge than females of similar size sampled earlier (Figure 6). It is probable that the larger females spawn at least twice during the summer, with less energy being available to produce eggs for a second ovulation. Further evidence for a second ovulation is apparent if the differences in ovarian weight during different periods of the

breeding season are considered (Figure 7). Early in the summer the ovarian weights of ovigerous females are much greater than they are later in the season for any particular body weight (although this difference is more pronounced in the larger size classes). Spent females were not observed from May through July, so we have no other indicator for frequency of ovulation. Rearing studies by Onizuka (1972) indicate that Kona crabs are ovigerous at least twice in succession each reproductive season. However, the sizes of the females that ovulated twice were not reported.

Females may indeed reach reproductive maturity at about 70-mm carapace length (Figure 8). However, other observations suggest a larger value for size at first reproductive activity. Ovarian size increases markedly with body size (especially in animals with carapace widths >80 mm or weighing >250 g; Figure 7). The estimate of mean minimum size of reproductive maturity (86 ± 8 mm; Figure 9) also indicates a larger size at first reproductive activity. The deviation between the theoretical expected values (broken line) and the observed values for larger females (Figure 9) would be expected if the animals ovulate more than once each breeding season (Wenner, Fusaro, and Oaten 1974). This is consistent with the statement by Onizuka (1972) that females may spawn twice in a season. Ovaries in smaller females may be too small to produce eggs for two ovulations, so they ovulate only once, resulting in a low percentage of ovigerous animals for these size classes in summer. The relatively small percentage of ovigerous females reported by Onizuka (1972) for Waialua and Waimea bays may be the result of a large number of females ovulating only once. The finding that sponges late in the breeding season are generally smaller than those earlier in the season indicates that the primary reproductive effort goes into the first ovulation. Whether or not a female ovulates a second time may be a response to food availability.

Ovarian growth for the summer breeding season is slow from September to February, after which it increases markedly. Since females plotted for 25 May had already ovulated, it can be assumed that the ovarian weights immediately prior to ovulation were higher than the postovulation ovarian weights (Figure 7).

Sexual Maturity

Since it is not uncommon for crabs to exhibit immature and mature instars (Pérez 1929; Ryan 1965; Haley 1969), we thought it worthwhile to determine if this is also the case with *Ranina ranina*. In order to do this, we had to obtain crabs <65 mm in carapace length, since we had already ascertained that crabs this size or larger are capable of ovulation. Eighteen crabs with carapace lengths <62 mm were caught and, although this is admittedly a small number, it may give an indication of the reproductive strategy of the species. Of the 18 crabs caught, 9 were the normal orange color and 9 were white. Dissection revealed that, in all but one case, white crabs were reproductively immature (small transparent gonoducts), whereas small orange crabs exhibited gametogenesis (Table 1). In all small orange females (Table 1), the ovaries were less than 1 g in weight and white in color, indicating that vitellogenesis had only recently begun and pigmented yolk had not yet been laid down. These could not be confused with spent ovaries, as the latter retain some yellow or orange color from residual ova.

As far as we know, this color difference has not been reported previously. Exoskeletons of both colors were equally rigid, so the white coloration is probably not due to a recent molt. This color difference could be of functional significance. A white animal living on white sand is well camouflaged. An orange coloration at the onset of puberty would facilitate intraspecific interaction associated with reproduction. (These small crabs and zoeal stage I are on file at the Bernice P. Bishop Museum, Honolulu.)

Onizuka (1972) reported that females with carapace lengths <58 mm lack maturing ovaries and are not ovigerous. Only two females in this study exhibited vitellogenesis prior to reaching this size. We feel that 65-mm carapace length is about the minimum size at which females may ovulate. This is also about the size at which the spermatheca becomes apparent. However, the smallest 5-mm size class in which at least 50 percent of the females are

TABLE 1

COMPARISON OF GONAD DEVELOPMENT IN SMALL INDIVIDUALS OF *Ranina ranina* (L.)

MALES		FEMALES	
CARAPACE COLOR AND SIZE (mm)	SPERMATOGENESIS	CARAPACE COLOR AND SIZE (mm)	VITELLOGENESIS
White		White	
31.9	no	35.4	no
34.0	no	42.3	no
37.3	no	Orange	
40.3	no	54.3	yes
40.5	no	57.6	yes
42.0	no	58.3	yes
42.6	some	60.7	yes
Orange		61.1	yes
43.6	yes, mature cells		
49.8	yes, immature cells		
52.7	yes, mature cells		
60.0	yes, immature cells		

NOTE: Small crabs are defined as being those of less than 62-mm carapace length.

ovigerous (during the spawning season) is 70.0–74.9 mm (Figure 8). By the method of Wenner, Fusaro, and Oaten (1974) (Figure 9), this mean minimum size at ovulation is about 86 ± 8 mm. Which value one chooses to work with depends upon the operation. Collectively, they provide a useful description of the range of minimum size at reproductive activity in females.

Onizuka (1972) made the assumption that males attain maturity at about the same size as do females. We found that males smaller than 60 mm (52.7 mm and 43.6 mm) in carapace length may have mature spermatozoa (Table 1). All males with carapace lengths >60 mm had mature spermatozoa in their reproductive tracts. However, the presence of mature spermatozoa does not mean that copulation has begun.

The change from white to orange probably is not associated with a distinct "puberty molt" (Pérez 1929). That term implies that the crabs copulate successfully after such a molt. In Kona crabs this color change appears to be associated with the onset of gametogenesis rather than with copulation.

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